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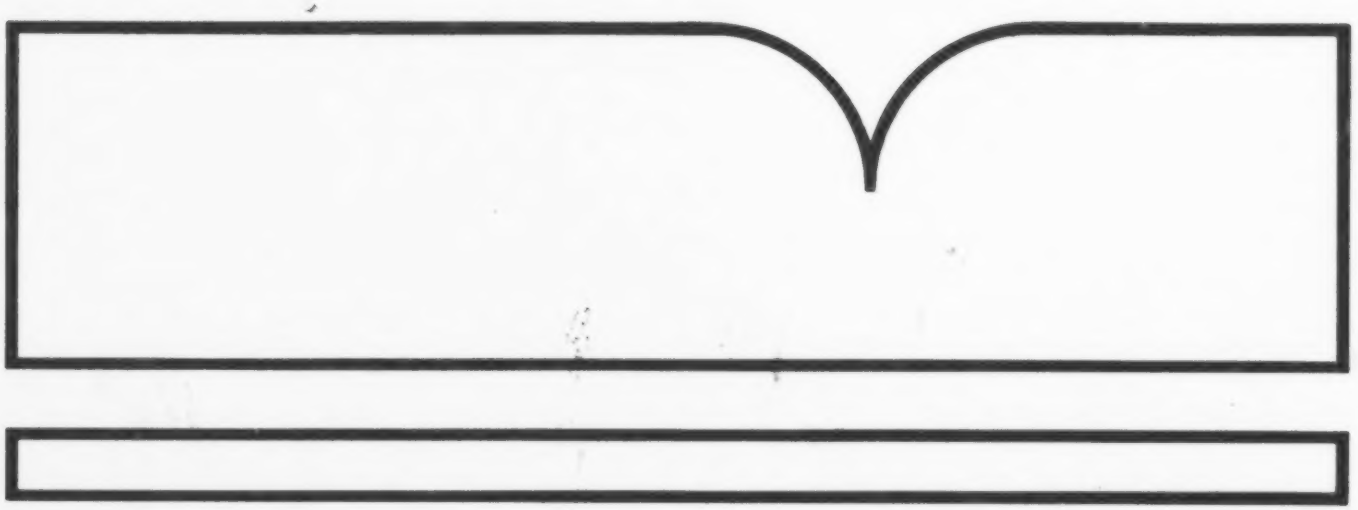

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16. ABSTRACT

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Modification of the Feeding Behavior of Marine Copepods by Sub-Lethal Concentrations of Water-Accommodated Fuel Oil*

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Abstract

The feeding behaviors of *Acartia clausi* and *A. tonsa* were measured in samples of water containing low levels of a water-accommodated fraction of No. 2 fuel oil. The copepods fed normally at a hydrocarbon concentration of 70 µg l^{-1}, but their feeding behavior was altered both quantitatively and qualitatively at a concentration of 250 µg l^{-1}. Three types of response to the higher oil level were found. The first was total suppression of feeding. Both other types involved suppression of feeding on particles between 7 and 15 µm diameter, but one showed no change in the ingestion of larger particles, whereas the other displayed increased feeding on particles larger than 15 µm diameter. These results suggest that the species of *Acartia* studied use three different modes of feeding, each on a different size range of particulate material. Low-level hydrocarbon pollution affects each feeding mode differently.

Introduction

Concentrations of petroleum hydrocarbons toxic to coastal zooplankton exposed for 1 to 7 days lie between 1 and 10 ppm for various pelagic species (Mironov, 1969; Kühnhold, 1977; Lee and Anderson, 1977; Lee and Nicol, 1977), and much higher for the tide-pool copepod *Tigriopus californicus* (Barnett and Kontogiannis, 1975). Corner *et al.* (1976b) have expressed some reservations about the studies of Mironov (1969), and effects of oil on individual species could not be determined from the results of Lee and Nicol (1977). The water-soluble fractions of fuel oil appear to be toxic at concentrations between 0.5 and 1 ppm (Lee, 1975). Narcosis occurs at lower concentrations than those that cause death (Lee, 1975), and precedes death at lethal concentrations (Gyllenberg and Lundqvist, 1976; Berdugo *et al.*, 1977). Although concentrations as high as 1 to 10 ppm are sometimes observed immediately under a spill, longer exposures of animals are likely to be at lower concentrations (Law, 1978), which may not be lethal.

Herbivorous zooplankton appear to be an important pathway by which petroleum hydrocarbons reach the benthic community. Fecal material is dense and sinks rapidly (Smayda, 1969), thus providing a rapid turnover of fine suspended matter to the benthos. Conover (1971) found that 20% of the bunker "C" oil in particulate form during the "Arrow" disaster arrived at the sediments in the fecal pellets of copepods. Feeding rate and fecal pellet production increase with temperature in some copepods, and would be expected to increase the rate of hydrocarbon input to the benthos. However, this may be reduced by the narcotizing effects of hydrocarbons on feeding rate. Corner *et al.* (1976a,b) and Harris *et al.* (1977) have shown that hydrocarbons enter copepods much more readily through their diet than from solution.

Berdugo *et al.* (1977) observed suppression of feeding, reduced fecundity and survival of the estuarine copepod *Eurytemora affinis* after short exposure to high concentrations (mg per liter) of the water-soluble fraction of fuel oil. They related these results to concentrations under a spill. Exposure to lower concentrations (10 to 50 µg per liter) of naphthalene caused no observable effects. Naphthalene alone was the least toxic of the water-soluble fractions tested by Berdugo *et al.* (1977), so the effects of chronic exposure to more toxic fractions (Lee, 1975) remain undescribed. The methods used by Berdugo *et al.* did not permit the measurement of qualitative changes in the feeding. The neritic copepods *Acartia clausi* and *A. tonsa* feed selectively (Allan *et al.*, 1977, Richman *et al.*, 1977), i.e., filtering rates as

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calculated by Gauld's (1951) formula differ with variations in the volume of particles present in different size classes. The mouthparts of copepods are abundantly supplied with chemoreceptors (Friedman and Strickler, 1975). *A. tonsa* feeding cannibalistically, and carnivorously selectively preys on other species (Lonsdale *et al.*, 1979). Tactile sensors on the body and chemical sensors on the mouthparts may both be involved in the determination of feeding behavior, and thus susceptible to interference by oil. Bigford (1977) observed that geotactic and phototactic behavior of larval crabs (*Cancer irroratus*) were altered by the water-soluble fraction of oil, and that pressure responses were slightly affected. Gyllenberg and Lundqvist (1976) observed disruption of locomotion in *A. bifilosa* and *Cyclops oithonides* after exposure to oil.

In this paper we describe the effects of low concentrations of No. 2 fuel oil on the feeding rates and selectivity of two coastal marine copepods.

Materials and Methods

The experiments were performed at the Marine Ecosystem Research Laboratory (MERL) at the University of Rhode Island (Kingston, R.I., USA). The facility consists of 12 fiberglass tanks, 1.83 m diameter and 5.49 m deep. Each tank contains about 13 m^3 of water above a 30 cm layer of mud. The sediment was taken from Narragansett Bay, Rhode Island, and contains a soft-bottom infaunal community. Bay water is pumped into the tanks at a rate which replaces all the water in about 30 days. The tanks are used as experimental ecosystems to test the effects of different environmental perturbations (Pilson *et al.*, 1979).

Three tanks were dosed with a water-accommodated fraction of No. 2 fuel oil twice weekly. Oil and tank water in a 1:1000 ratio were shaken together for 5 min, then allowed to stabilize for 30 min. At the end of this period, the aqueous fraction was added to the tanks. The hydrocarbon level in the tanks varied from about 250 ppb (µg l^{-1}) after an oil addition to about 70 ppb just before the next addition. Water samples taken directly before and after the addition of oil varied little in particulate content.

Whenever possible, *Acartia clausi* and *A. tonsa* were collected by net tow from the tank to be tested. However, low copepod densities in the oil tanks often made this impractical. In such cases, individuals were taken from a control (non-oil) tank or Narragansett Bay. Copepods to be used in feeding studies were rinsed three times with experimental water before being pipetted with a minimal amount of water into 125 ml feeding bottles. All experiments were carried out with adult or late copepodite stages of female *A. clausi* and *A. tonsa*. The copepods were generally used within 6 h of capture, and never held more than 24 h before use.

Experimental water was siphoned from a tank and passed through a Nitex sieve (pore size 153 µm) to remove large individuals, before being divided between bottles. Copepods were added to one bottle, leaving a second bottle as a control. All experiments were run at ambient temperature (ca. 3° to 22 °C) in the dark for about 18 h. The bottles were rotated end-over-end at 1 to 2 revs/min to prevent the settling of particulate material. A small (less than 1 ml) air bubble was left in each bottle to increase mixing. The number of copepods added to a bottle was varied with the temperature to result in the smallest change between the control and experimental bottles that could be observed with statistical certainty. The volume per individual ranged from about 10 ml at low temperatures to about 30 ml at higher temperatures.

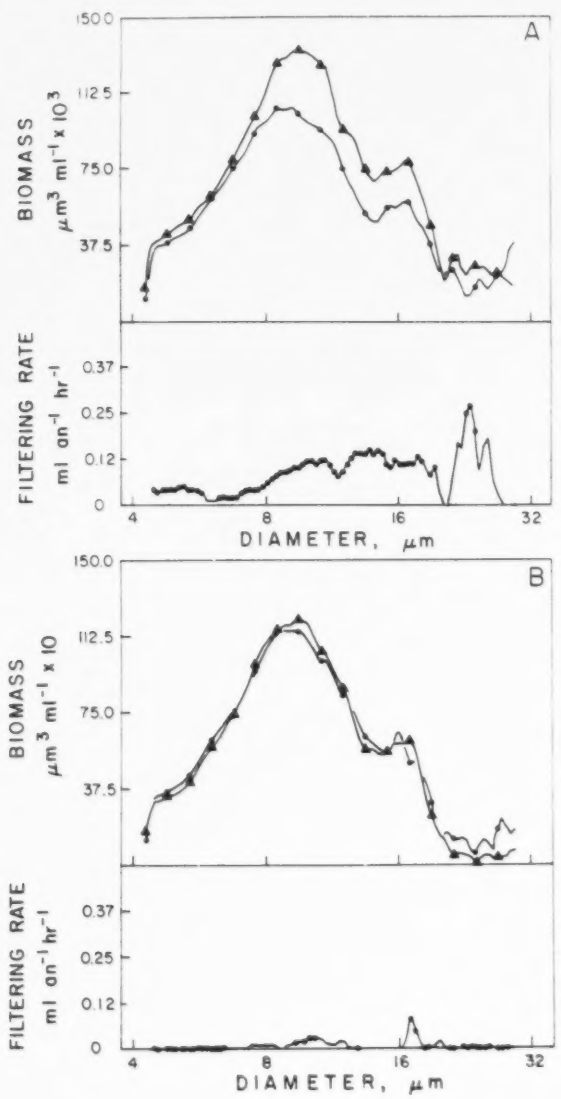
At the end of the experimental period, the contents of the bottles were poured through a 74 µm stainless steel sieve to remove the copepods and particles large enough to clog the aperture of the particle counter.

Three replicate analyses were made on each sample, using a computerized Particle Data Corporation (Elmhurst, Illinois) counter, fitted with a 95 µm aperture. This system records about 100 discrete size classes (channels) between 4 and 30 µm esd (equivalent spherical diameter–the diameter of the sphere of equal volume). Data reduction was carried out as described by Richman *et al.* (1977).

Results

Three major types of response to oil stress by *Acartia clausi* and *A. tonsa* were observed. Fig. 1 shows the most simple of the three. This experiment was run at 10 °C using *Acartia clausi*. The upper graph of Fig. 1A shows feeding behavior in water shortly before an oil addition, when the hydrocarbon concentration was about 70 ppb. The major peak in biomass in the mid-range of this plot is a pattern typical of Narragansett Bay when diatoms are abundant. The filtering rate (lower graph, Fig. 1A) was calculated from Gauld's (1951) formula, and is equivalent to Frost's (1972, 1975) clearance rate. A point on the filtering rate curve indicates significant feeding, i.e., the difference between the control and experimental counts on that channel is significant at the 95% confidence level. Significant feeding was continuous over most of the range examined, and selection was for the large particles rather than the biomass peak (Fig. 1A). Fig. 1B illustrates the same experiment with water taken just after the addition of hydrocarbons. The biomass curve for the control bottle is similar to that in Fig. 1A, but the filtering rate curve displays a marked difference. Petroleum hydrocarbons, in concentrations of about 250 ppb caused a total suppression of feeding, a result not found with a concentration of about 70 ppb. This response was recorded in 3 out of 14 experiments with the two *Acartia* species.

A second experiment used *Acartia clausi* at 5 °C (Fig. 2). The filtering-rate curve for the sample collected before an oil addition (Fig. 2A) was considerably lower than in the previous experiment, due to the lower concentration of particulate matter and the lower temperature. There



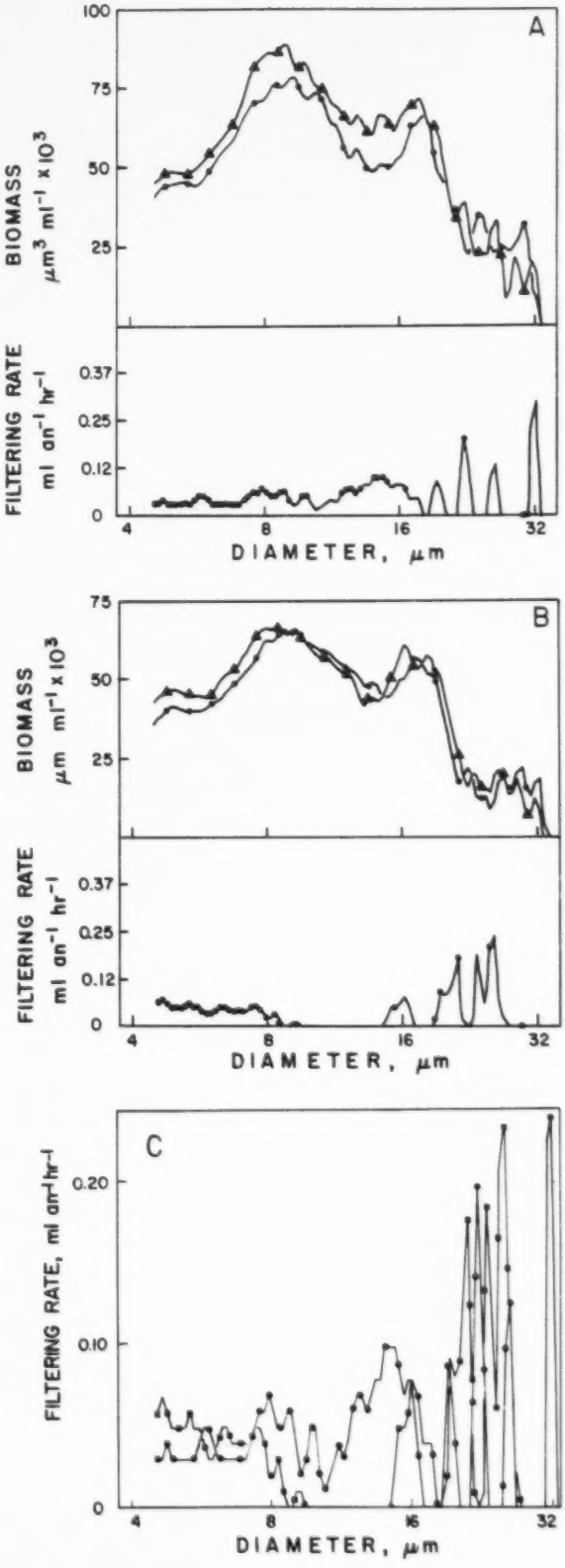


Fig. 1. *Acartia clausi.* Feeding before (A) and after (B) an oil addition at 10 °C. Upper graphs of (A) and (B) show particle size-biomass distributions, where trianges = controls and circles = experimental distributions after feeding. Lower graphs give filtering rate as a function of particle size; the points on the filtering rate-curve indicate when concentrations in control and experimental bottles were significantly different. an = animal (copepod)

Fig. 2. *Acartia clausi.* Feeding before (A) and after (B) an oil addition at 5 °C. Upper graphs of (A) and (B) show biomass distributions, where triangles = controls and circles = experimental distributions after feeding; lower graphs give filtering rate as a function of particle size. (C) Filtering rate curves from (A) and (B) plotted on the same axis, where circles = feeding before oil addition and squares = feeding after oil addition, symbols on the filtering rate curves in this graph only are to identify the lines and do not denote significance of feeding.

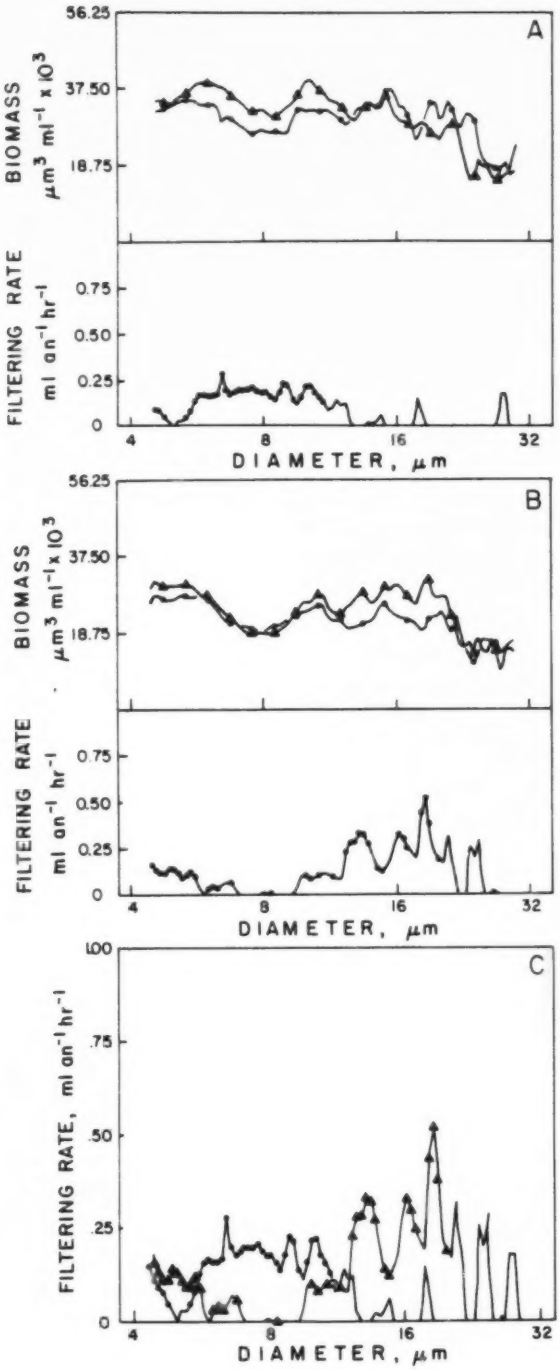


Fig. 3. *Acartia tonsa.* Feeding before (A) and after (B) an oil addition at 22 °C. Graphs of (A) and (B) show size-biomass distributions, where triangles = controls and circles = experimental distributions after feeding; lower graphs give filtering rate as a function of particle size. (C) Filtering-rate curves from (A) and (B) above plotted on same axis, where circles = feeding before oil addition and triangles = feeding after oil addition

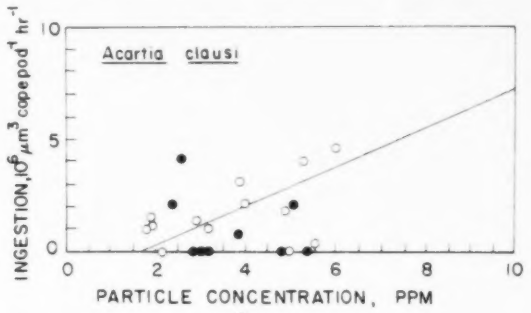


Fig. 4. *Acartia clausi.* Ingestion rate versus concentration of particulate material. Regression line is for ingestion from Narragansett Bay water, open circles from MERL oil tanks at 70 g l^{-1} hydrocarbons, and filled circles from MERL oil tanks at 250 g l^{-1} hydrocarbons

was, however, significant feeding on particles up to 16 µm esd. After the addition of oil there was no significant feeding on particles from 8 to 15 µm esd (Fig. 2B). The apparent particle production in this size range was not significant. Fig. 2C gives the filtering-rate curves for the two parts of this experiment plotted together on the same axis. The curves coincide below 7 µm and also above 15 µm esd, showing that the only difference in feeding behavior caused by the increase in the hydrocarbon level was the suppression of feeding on particles in this medium size range. This response was observed in 4 out of the 14 experiments.

The third type of response was observed in an experiment with *Acartia tonsa* at 22 °C (Fig. 3). The biomass of the particulates was lower than in the previous examples, and the well-defined diatom peak was absent (Fig. 3A). This pattern is typical for Narragansett Bay in the summer when the particulate material is mostly microflagellates and detritus. Although there was significant feeding on the small particles, those over 12 µm were essentially untouched (Fig. 3A). After the oil was added (Fig. 3B), there was significant feeding on particles up to about 20 µm esd. Not only was the feeding on the large particles enhanced, but feeding on the middle range of particles (6 to 13 µm esd) was depressed (Fig. 3C). In this third type of response, as in the second type, feeding on the very small particles was largely unchanged by the increase in hydrocarbon concentration. The third type of response was noted in 4 out of 14 experiments.

Although variation was great, ingestion rates of *Acartia clausi* were best-fit (least-squares) by a linear function of total biomass of particulate material (Fig. 4). The regression line is described by: $I = -0.148 + 0.087\,C$, where I is ingestion and C is particle concentration. The percentage of variation explained by the regression (R^2) is 80.3%. The data upon which the regression line is based are not shown in Fig. 4. The open circles represent the ingestion rate for *A. clausi* feeding in water taken from MERL oil tanks just before an oil addition. These points follow the observed Narragansett Bay pattern with few exceptions. Some experiments resulted in negative ingestion rates. These were interpreted as total lack of feeding

and are plotted on Fig. 4 as zero ingestion. Only two of the points before oil addition show this result, and one of these is close to the predicted threshold biomass value. The filled circles in Fig. 4 reflect the ingestion rates on water samples taken less than 24 h after an oil addition. There was no feeding in over half these cases, and the correspondence of the data with the regression line has broken down. These results suggest that the copepods fed normally, from a quantitative point of view, at the lower hydrocarbon concentration used in this study (before oil addition) but often had lower ingestion rates within 24 h after the addition of fresh oil.

Discussion

The filtering-rate curves for *Acartia clausi* and *A. tonsa* grazing on water samples taken before an oil addition (Figs. 1A, 2A, 3A) show the same types of relationships with the biomass curves as found by Richman *et al.* (1977) for various copepods feeding on Chesapeake Bay water with no added hydrocarbons. Thus, the feeding behavior on the water samples taken before oil addition in this study probably represents the normal feeding behavior of the copepods. Alteration of the feeding behavior after an oil addition need not be due only to the increase in the hydrocarbon concentration from 70 to 250 ppb. Gearing *et al.* (1979) reported that, throughout much of a long-term MERL oil experiment, the low-molecular weight aromatic fraction of the hydrocarbons, such as the benzenes and naphthalenes, were lost from the water column faster than the decrease in total hydrocarbons. Thus, the composition of the hydrocarbons changed as well as the total quantity.

Although much of the data presented in this paper was obtained using *Acartia clausi*, no consistent difference was found between its behavior and that of *A. tonsa*. For example, it has been demonstrated that linear relationship exists between ingestion rate and total particulate material in the water for several species of copepods (Mayzaud and Poulet, 1977), including *A. tonsa* (Reeve and Walter, 1977). In addition, the qualitative changes in the feeding of *A. tonsa* were similar to those in *A. clausi*.

General suppression of feeding and other metabolic activities by copper were shown by Reeve *et al.* (1977a,b). While Reeve *et al.* (1977a) did not demonstrate qualitative changes in feeding behavior on natural food, the clearance rates they observed with standard food (panel c of their Fig. 3) suggest results similar to ours, particularly at about 10 µm esd. The reduction in grazing pressure on 7 to 15 µm particles and the increase in grazing on larger particles which we observed (Figs. 1-3) could lead to increases in the relative proportion of small species of phytoplankton to larger diatoms. This type of response has been observed in other experimental systems (Parsons *et al.*, 1976; Menzel, 1977; Thomas and Siebert, 1977).

The results described in this study indicate that in 11 out of 14 experiments, addition of hydrocarbons to a level of 250 ppb causes at least partial suppression of feeding, similar to the observations of Berdugo *et al.* (1977). However, the hydrocarbons affect feeding on the large (> 15 µm esd), on the mid-size (7 to 15 µm esd) and on the small (< 7 µm esd) particles to different extents. This suggests that different feeding modes may be used by *Acartia* spp. to capture particles in different size ranges.

The minimum intersetule distances in adult *Acartia* species are between 7 and 10 µm (Conover, 1956; Nival and Nival, 1976). Thus, the smallest particles that could be filtered passively have diameters of about 7 µm. This diameter corresponds to the lower limit of our mid-range, suggesting that filter-feeding is adopted for particles between 7 and 15 µm diameter. This conclusion is supported by the work of P. Donaghay (personal communication), who found that *A. clausi* feed raptorially on particles larger than 15 µm. It is important to note that filter-feeding is associated with the size spectrum that is most affected by the addition of hydrocarbons. The three types of response to oil addition which we recorded all exhibited suppression of feeding in this size range. Friedman and Strickler (1975) and Poulet and Marsot (1978) have demonstrated that copepods use chemoreception in their feeding behavior. Assuming that one effect of the hydrocarbons in these experiments was to interfere with the sensory processes used in feeding, it is possible to conclude that chemoreception is used primarily in conjunction with the filter-feeding mode. Chemical alteration of prey selection has also been noted in fish (Farr, 1978), where contact chemoreception appeared to be an important mechanism.

Raptorial feeding, which may be triggered by physical contact with a large particle, was less sensitive to hydrocarbon stress (Figs. 2 and 3). This type of feeding sometimes increased in the samples taken after oil addition, perhaps to compensate for the loss of ingestion in the filter-feeding range (Fig. 3). These results suggest that chemoreception is not of prime importance in this mode of feeding, although Poulet and Marsot (1978) have shown that the copepods are capable of discrimination on the basis of chemical factors with particles of 50 µm diameter.

The mode of feeding that accounts for the ingestion of very small particles is not clear. Although hydrodynamic mechanisms have been suggested that would allow animals to filter particles smaller than the nominal mesh size of their filtering appendages (Rubenstein and Koehl, 1977), it is doubtful that these provide the complete explanation. M. Roman (personal communication) has found *Acartia tonsa* capable of ingesting bacteria and detritus particles as small as 1 µm diameter. It is difficult to explain this without hypothesizing a new feeding mechanism for them. As a possible answer, Roman (personal communication) suggests aerosol suspension feeding (La Barbera, 1978), whereby small particles are caught in mucus and ingested as a larger bolus. The heterogeneous nature of the bolus would argue against the efficiency of selective feeding by this mode. Rejection of a whole bolus on the basis of one unpalatable

particle could result in the loss of several nutritious particles after the energy involved in capture had already been expended. Whether by this mechanism or another, feeding on small particles was largely unaffected by the levels of hydrocarbons used in this study.

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